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Geographical distribution of the marine spermatophytes

WILLIAM ALBERT SETCHELL

The marine spermatophytes belong to two nearly related families, the Hydrocharitaceae and the Potamogetonaceae. The members of both families are aquatic, either inhabiting the fresh waters or those which are brackish or marine. Of the first family, the Hydrocharitaceae, there are three genera, *Halophila*, *Enalus* and *Thalassia* which are marine, while of the second family, the Potamogetonaceae, there are five marine genera, viz., *Zostera*, *Phyllospadix*, *Cymodocea*, *Diplanthera* (or *Halodule*) and *Posidonia*. Of these eight genera, I find thirty-four or thirty-five species at present enumerated. Undoubtedly much is yet to be learned concerning the marine spermatophytes since they have not been so generally collected and studied as other spermatophytes because of their habitat. The greater number of the species, in fact all except the three species of *Phyllospadix*, so far as I am aware, live in shallow water (down to not over 10 fathoms usually) and are seldom if ever uncovered by ordinary low tides. Such localities are seldom visited or collected over by botanists other than phycologists and the latter are usually in search of "other game." There are only two botanists who have given special attention to the marine spermatophytes, viz., P. Ascherson and C. H. Ostenfeld. The former interested all explorers, travellers and navigators possible in these plants and obtained much that was valuable as a result of his and their efforts. As early as 1867, Ascherson published a preliminary account of the marine spermatophytes as then known. He published supplementary accounts in 1870, 1871 and 1875. Finally he contributed the account of the marine genera to Engler and Prantl's "Pflanzenfamilien" (1889) and of the marine species of the Potamogetonaceae to Engler's "Pflanzenreich" (1907). In 1871, Ascherson also discussed the geographical distribution of the "sea-grasses," as he designated the marine spermatophytes and later (1906) issued a revision of this article bringing the information and discussion up to date. The greatest credit is due to Ascherson for following up the subject for so many years and with such vigor as well as for the very satisfactory way in which he has treated these little-known plants. Within comparatively recent years Balfour (1878) has written concerning the morphology of *Halophila* and Rydberg (1909), concerning the morphology of *Thalassia testudinum* Solander, while Ostenfeld (1905, 1908, 1909 and 1916) has contributed several papers dealing with the morphology, taxonomy and ecology of members of both families of marine spermatophytes.

The ecology, or topographical distribution, of the marine spermatophytes is fairly simple and more or less uniform in the principal details. They all grow in shallow water, that is from about high-water mark down to ten fathoms and possibly in exceptional cases even somewhat deeper. The species of *Phyllospadix* are usually inhabitants of the lower and even middle littoral belts, but they differ in other details of their ecology from the rest of the marine spermatophytes (cf. Dudley, 1893, p. 415). The species other than those of *Phyllospadix*, are inhabitants of the upper sublittoral belt and are seldom completely uncovered unless it is at the time of extreme low-water. The species, also with the exception of those of *Phyllospadix*, at least so far as known to me, prefer comparatively quiet water and are most often found in sheltered places although some, at least, are found in runways where there may be at times fairly swift and strong currents. The species of *Phyllospadix*, on the other hand, prefer localities within the littoral belt where they are exposed to strong wave action and foaming surge (cf. Dudley, 1893, p. 415) and may be classed as typical "surge-plants" or "cumaphytes." As to substratum, the great majority of the species grow with their long and prostrate rhizomes buried more or less deeply in the sand or mud, but *Posidonia oceanica* and the species of *Phyllospadix* inhabit rocky, or stony, ground and have comparatively short and more or less erect and condensed rhizomes. The method of dissemination of *Phyllospadix* is one of the very few of those of the marine spermatophytes known. This was worked out in the botanical laboratory of the University of California a number of years ago by Ralph E. Gibbs (1902). He was the first to describe the ripened and detached fruits. After the pulpy exocarp is worn away from the ripe drupe-like fruit, there remains the black horn-like mesocarp exposed to view. The fruit, in this condition, looks like the head of some large beetle with two projecting and inwardly curved but unjointed antennae, or possibly mandibular structures. The inner edges of these arms, which come off at an acute angle from the sides of the flattened turbinate main body of the fruit, have inwardly and upwardly pointing stout fringing bristles. By means of these arms and their bristly armature, the fruit, floating in the waves may grasp a jointed coralline on the otherwise bare and smooth rock and tightly cling to it. It may also germinate in position on the coralline and, as the rhizome develops, it sends out a quantity of stout roots from each segment. The roothairs, which are produced in abundance, attach themselves to the rocks and also catch and hold floating sand, and this process continues as the rootstock goes on developing until a small patch of sand is formed about the developing plant. A small beach may thus be formed among the rocks. This behavior makes it evident by what method the *Phyllospadix* obtains its foothold and maintains it on the exposed rocky shores where it, alone of all the marine spermatophytes, can make its home. The mud- and sand-inhabiting species are distributed over wide areas by the plants and portions of plants, especially those having portions of the rhizomes or ripened or ripening fruits, which are torn away, or dislodged in some fashion, and float long distances, as happens so constantly and on such a large scale in the case of *Zostera marina* (cf. Ostenfeld, 1908, p. 6, 15) and in very special form in *Cymodocea antarctica* (cf. Tepper, 1881). As to the salinity and specific gravity of the water in which the marine spermatophytes grow, it is probably enough to state that the designation "marine" is intended to convey that the plants included are inhabitants of salt as distinguished from brackish water and that the variation in salt content is comparatively slight (cf. Ostenfeld, 1908, p. 17, and Osterhout, 1917).

The topographical conditions and considerations just enumerated have to do with the various marine spermatophyte or "*macro-enhalid*" formations and associations found in various zones, regions, provinces and districts of the marine flora, but it is the intention of this paper to inquire rather into the climatic distribution of the marine spermatophytes and to compare it with the distribution of the marine algae: In attempting to do this, I shall try to arrange the different species in the climatic zones already outlined by me in previous papers (1915, 1917). These climatic zones are as follows:—Upper Boreal and Upper Austral of mean maximum temperatures from 0°–10° C., Lower Boreal and Lower Austral 10°–15° C., North Temperate and South Temperate 15°–20° C., North Subtropical and South Subtropical 20°–25° C., and Tropical from 25° C. mean maximum up to the limit of 29° or 30° C. It seems that the marine spermatophytes ought to follow the same temperature laws as the marine thallophytes and be found in similar zones and just as closely restricted in their distribution. The algae, so far as I am able to determine at present, are either restricted to a single zone or, if they extend from one zone into others, invade the additional zones because, for some reason or other, they find in the invaded zone, or zones, the temperatures characteristic of the zone to which they are normal. The reasons for suspecting invasion, even when the data are not completely at hand for proof is the existence of warm areas, spots and particularly of seasonal minima in warmer zones each with its peculiar flora. Since the marine spermatophytes inhabit the shallow waters, the criteria of their distribution may be considered to be the mean maxima and minima of the surface waters 5° C. apart, as it is in the case of the great majority of the marine algae.

The climatic distribution of the marine spermatophytes has been treated of by Ascherson as I have already mentioned. In 1871, he published his paper on this subject and discussed and represented on maps the distribution of the twenty-two species then known to him. In distribution by oceans, Ascherson credits one species to the Arctic Ocean, seven to the Atlantic, fourteen to the Indian Ocean and thirteen to the Pacific Ocean. The Antarctic Ocean has no species credited to it. Ascherson discusses the relation of the different species to the climatic zones as laid off with reference to the Arctic Circle and the Tropics of Cancer and Capricorn. Such a discussion of climatic distribution does not lead very far even in connection with land plants, since the relation either to isotherms or to the total amount of heat obtained is not shown with any exactness. Ascherson, also, in charting the distribution, simply draws a continuous line between the extreme records and makes an enclosed area as if of continuous occurrence and of possibly uniform frequency. The results are, consequently, confusing and misleading. It is, nevertheless, a simple matter in the case of the strictly tropical species. They are in the great majority among the marine spermatophytes and are clearly shown as inhabitants of the warmer, or even of the warmest waters of the oceans. The distribution in cases of the smaller number of inhabitants of the temperate zones, as these are understood and marked off on the ordinary maps seems also plain, although here it is difficult to understand in the case of certain of these species why they do not fill out their "zones" more completely. One species, however, shows such an extensive distribution as to cause special remark on the part of Ascherson. This is the common "eel-grass" of our Atlantic coast, *Zostera marina*. As plotted by Ascherson, this species extends from the Kara Sea (to the northwest of Asia) down to Cadiz in Spain, from Iceland to Newfoundland (avoiding Greenland) and thence down the eastern coast of the United States to western Florida, from Bering Strait to and including Yakutat Bay, Alaska, and from the same strait down along the east coast of Asia through the Loo Choo Islands nearly, but not quite, to Formosa. Such an extensive distribution might well disturb any ideas of limits of distribution at all narrow.

In the revised reprint of his paper, issued in 1906, Ascherson lists thirty-two species of marine spermatophytes, an increase of ten over the earlier issue, some of which had resulted from segregation from species listed before, and also expresses doubt as to the extreme limits of the distribution of *Zostera marina*. He still lays stress, however, on the circles and the tropics in their relation to the distribution of the individual species.

In 1907 Ascherson contributed the accounts of the marine spermatophytes, so far as published, to the "Pflanzenreich" of Engler, and Ostenfeld, in 1902, published a preliminary revision of *Halophila*. From these, as well as from other sources, it seems that some thirty-four or thirty-five species are now to be recognized. Of these eighteen are confined to the tropical zone of marine waters as I have attempted to limit it by including only those waters of a mean maximum temperature of 25° C. or above, four to subtropical zones in that they inhabit marine waters of a mean maximum of 20° to 25° C., while four are inhabitants of strictly temperate zones, whose mean maxima range from 15° to 20° C. These twenty-six species certainly seem typically stenothermal, being limited to zones of amplitudes of 5° C., for the hottest month of the year, as to their persistence. The remaining eight species are reported as extending over two or more zones (of 5° C. mean maxima each) and consequently, therefore, more or less eurythermal. Of these one species is credited with occupying both tropical and subtropical zones, five species with occupying both subtropical and temperate zones, one species as occupying tropical, subtropical and temperate zones, while one species is credited with occupying both boreal zones as well as temperate, subtropical and tropical zones or five zones in all. The last species is, if properly referred to all the zones it is said to inhabit, a most typically eurythermal species. It seems best, however, to inquire into the particulars of the distribution of these seemingly eurythermal species and to attempt to determine so far as possible the exact conditions underlying the attributing to them of such extensive ranges.

The cases of species credited with inhabiting two zones do not seem very difficult of explanation on a strictly stenothermal basis. In other words, such species may be found to belong strictly to one or other of the zones they inhabit and invade the second zone only because they find at certain places, or at certain seasons, the same heat conditions that they need and find in the normal zone. To examine into difficult cases, we may select *Zostera capricorni* Ascherson, which is said to extend from Cape York in tropical eastern Australia to Port Jackson in subtropical eastern Australia. It will needs be uncertain until this species is better known, as to just which zone is to be considered normal for this species, but the distribution indicates that the South Subtropical Zone is the normal zone since *Z. capricorni* extends only partially into the Tropical Zone. The invasion of the Tropical Zone, in this case, may be seasonal and this supposition is strengthened by observing that the isocryme, or line of mean minimum temperature for 25° C., touches the coast of eastern Australia in the vicinity of Cape York. In the cases of the five species which are credited to both a subtropical and an adjacent temperate zone, two of these species, viz., those belonging to the genus *Phyllospadix*, are not certainly members of the flora of the subtropical zone and also are inhabitants of the littoral belt where temperature relations are complicated by the influence of air temperatures and considerable insolation at periods of low water. It may be for these reasons that these two species also extend into the Lower Boreal Zone as is indicated by some statements as to their distribution. Two other of the two-zoned species are mud and shallow-water species and probably are normally subtropical, extending over into spots in the temperate zone where the combination of shallow quiet waters and higher air temperature allows the air and the sun to raise the temperature of the water some 5° C. or even more, for a sufficient length of time each season or, at least in an occasional season of fairly frequent occurrence. The two species just referred to are *Zostera nana* Roth and *Z. pacifica* S. Watson. It may also be mentioned here that it is by no means sufficiently certain as to the exact limits of the distribution of either of these two species. The fifth species of this two-zoned group is *Cymodocea antarctica* (Labill.) Endl. This species occurs on the western as well as on the southern coasts of Australia and on the northern shores of Tasmania. This seems likely, for similar reasons to those advanced in the case of *Zostera capricorni*, to be a case of seasonal invasion of the South Subtropical Zone from the South Temperate Zone. It may be, however, an invasion in just the opposite direction, viz., from the South Subtropical to the South Temperate Zone, since according to Tepper (1881) the South Temperate plants increase only by a peculiar and specialized vegetative splitting off of buds or short branchlets.

The cases of species credited to three or more zones are more complex if we undertake to show that, in spite of this extended distribution, they are to be regarded as steno- rather than eurythermal. There are two of these, at least at present, considered to be of very extensive distribution, viz., *Halophila ovalis* (R. Br.) Hook. f. and *Zostera marina* L. The first seems to center in the tropics of the Red Sea, the Indian Ocean and the tropical portions of the western Pacific. It extends also around Australia and to the northern portion, at least, of Tasmania. The second species is more characteristic of the northern hemisphere, extending southward from the arctic regions to the tropics both on coasts of the Atlantic and the Pacific. The second species, however, seems to be rare in both the tropics and in the frigid zones and probably has its center of distribution in one or other of the intermediate zones. It seems best to examine the facts concerning both of these species in some detail.

The first species of this really extensive distribution to be considered is *Halophila ovalis* (R. Br.) Hook. f., which is generally credited with being widely distributed through the tropical portions of the Red Sea, Indian and Pacific Oceans. It also extends entirely around the continent of Australia and occurs on the shores of Tasmania touched by Bass Strait. The extensive distribution in the tropical waters seems to mark this species as normal to the Tropical Zone, although it may be questioned as to whether one or more species are included, even here, under the name, since in 1909, Ostenfeld separated the plant of the Marianne and Philippine Islands as a separate species under the name of *Halophila ovata* Gaud. If the determinations are correct, however the occurrence of *H. ovalis* on the coasts of Australia extends the distribution through the South Subtropical into the upper portion of the South Temperate Zone. This would mean the endurance of temperatures from at least 18° or 19° C. upwards to about 29° C. It is manifestly impossible to do more than to discuss a case like this and to suggest possibilities as to how a species, whose lower limit of temperature persistence may be supposed to be 25° C., may exist in localities where the mean maximum is indicated as about 18° C. or at most 19° C. There are, however, several possibilities which might be investigated by those having an opportunity of studying the living plants. In the first place, the plants of the Australian and Tasmanian coasts are sterile, or, at least, have not been found in other than vegetative condition. It may be that the plants of these countries are of a different species from those of the tropics. In opposition to this, it may be said that Ostenfeld credits this species, with which he is presumable familiar, to the coast of Western Australia as late as 1916. His plants, however, were sterile. In the second place, this matter of the sterility of the Australian and Tasmanian specimens which seems to be the general testimony from Bentham in 1878 (vol. 7, p. 183) on to Ostenfeld in 1916, may indicate that this southern extension of the range is composed of plants which never fruit and which possibly increase in number and, therefore persist, through vegetative multiplication only. Unfortunately, there is too little information as the habits and methods of dispersal of this species, but it is extremely likely that vegetative methods of propagation may be important in the establishment and persistence of this species. The third and possibly the most probable alternative is that the shallow cooler waters inhabited by plants of this species, may through the higher temperature of the air and through insolation be raised six or eight or even more degrees in temperature for a sufficient number of days or weeks to enable the plants to flower and to ripen their seeds. This amount of increase of the temperature of shallow protected waters is known to occur. While no one of these three possibilities can be demonstrated to be actually in operation, yet there seems to be sufficient reason for not regarding the extensive distribution of this species as indicating a eurythermal character so far as persistence through seed-reproduction is concerned. That the species in general is eurythermal, may be granted, since the sum total of its endurance extends over a greater interval than 5° C. or even 10° C. We may suspect, however that there is very little vital activity during the lower periods of temperature experienced, but the ability to withstand such lower temperatures in a condition of quiescence or rigor. In other words, such a seeming eurythermal species as this probably is able to endure a period of hibernation while the other strictly tropical species of *Halophila* are not. A second assumption in the case of *Halophila ovalis* is that it is a perennial species, as its whole appearance and general structure indicate.

The second and other species of marine spermatophyte credited with extensive distribution is the common eel-grass or grass-wrack, *Zostera marina* L., of the northern hemisphere. The distribution of this species, as generally given, extends from high north (at least Lower Boreal Zone) to well within the Tropical

Zone (Florida and the Riu-Kiu Islands). This is certainly a perennial species and one capable of wide dispersal. It seems to be readily dislodged from the sand or mud in which its rhizomes are buried and floats long distances because of the gases contained within the numerous air-passages within its leaves. There is good reason, also, for suspecting that two, or even three, distinct genetic entities are included under this specific name, if not at least two distinct taxonomic species. The typical *Zostera marina* is generally considered to be the flat- and broad-leaved form while a variety with somewhat shorter, narrower and thicker leaves is called var. *angustifolia* Hornemann. There seems also to be a form intermediate between the two and this corresponds, in part at least, to f. *stenophylla* Aschers. & Graebner. The species and var. *angustifolia* often occur together, but apparently always separated according to substratum and somewhat possibly according to depth, the variety in a belt above that occupied by the species and restricted to a firmer substratum. Ostenfeld, in 1908, made a series of studies and careful measurements of these various forms and came to the conclusion that the differences were the results of more favorable *vs.* less favorable environment. I am inclined to suspect, nevertheless, that there are at least two genetically distinct varieties, or even species, which overlap in their distribution, the narrow-leaved variety preferring shallower water and firmer substratum than the broader-leaved form (or forms) and being able to extend farther into the areas of colder waters than the broader-leaved forms. Very little seems to have been done as yet as to the collection and study of the flowers and fruits, and especially of ripe seeds, at various localities in the range and this leaves much to be desired especially as regards seasonal data.

On the coasts of Europe, *Zostera marina*, in one form or another, has been given a range from Iceland and the extreme north of Europe to and including the Mediterranean Sea, but, as near as I am able to determine, the extreme northern locality, viz., White Island in the Kara Sea is based on the report of a non-botanist (cf. Ascherson, 1906, p. 402). It seems to stop, so far as general and continuous distribution is concerned, at Tromsoe, Norway, or somewhat below, but does occur in the Varanger Fiord and in Porsanger Fiord and in the White Sea on the northern coast of

Europe. These northern plants seem to belong to var. *angustifolia* (cf. Blytt, 1861, p. 1278). *Zostera marina*, in the extended sense seems to be fairly continuous along the western coast of Europe down to the neighborhood of Cadiz in Spain, while in the Mediterranean Sea it is less common and of spot-wise occurrence. It occupies, therefore, so far as the European coast is concerned, the Lower Boreal and North Temperate Zones without question and probably also extends discontinuously into the Upper Boreal and the North Subtropical Zones.

On the eastern coast of Asia, *Zostera marina* extends from somewhere near the Bering Strait south to and including some of the Riu-Kiu (or Loo Choo) Islands, thus occupying the Upper and Lower Boreal, the North Temperate, the North Subtropical and the upper portion of the Tropical Zones. I am unable to find out very much concerning the details of distribution on the Asiatic coasts. The relation of *Z. japonica* Aschers. & Graebner (1907, p. 32) to cited references is not clear. Turning to the eastern coasts of the North Pacific Ocean, it is reported from Port Clarence, Alaska, and from various localities along the coast south to Catalina Island, California, thus occupying the Upper Boreal, Lower Boreal, North Temperate, and possibly also entering the North Subtropical Zones. [*Z. oregona* S. Watson is not recognized by Ascherson and Graebner, but is referred to *Z. marina* (cf. Ascherson, 1906, p. 402).]

The data as to the distribution of *Zostera marina* along the eastern coast of North America are the most extensive and exact of any immediately accessible to me and, consequently, I shall lay more stress upon them. They are, however, by no means sufficiently comprehensive to form a satisfactory basis for an opinion, as I shall attempt to indicate. There is little doubt but that some form of it has been found in the inner portion of Pisigsarfix Fiord, at lat. 64° 35′ N. on the coast of southwestern Greenland (cf. Lange, 1887, p. 282). The species and its variety *angustifolia* reappear at the Strait of Belle Isle, no records being available of its occurrence on the intervening coast of Labrador. It is evidently abundant in the Gulf of St. Lawrence and along the coast of New England to New York Harbor. There is plenty of specimens to show the distribution from Newfoundland to New York divided between the Gray Herbarium and that of the New York Botanical Garden. The specimens of the southern portion of this part of the range are largely, although not entirely the broader form of the species. Both Britton (1881, p. 100 and 1889, p. 259) and Stone (1911, p. 166) say that it is common in all bays along the coast of New Jersey, although the latter adds that it has not been found on the New Jersey shore of Delaware Bay. Stone also states (*loc. cit.*) that it has been observed in flower and fruit only in June and this is confirmed in a letter from Bayard Long, while above Cape Cod it is in fruit in August. I have not found a specimen in either the Gray Herbarium or that of the New York Botanical Garden from any part of our eastern coast south of New York Harbor. It is reported as frequent in shallow water in Chincoteague and Chesapeake Bays on the coast of Maryland by Shreve, Chrysler, Blodgett and Besley (1911, p. 395), and there is certain report of it as growing in abundance on the northern stretch of the coast of North Carolina. The only locality reported south of North Carolina is that of West Florida. This was made by Chapman (1860, p. 444) and repeated by Small (1913, p. 41), but I can find no specimen to verify it. Ascherson, in his later paper on the distribution of the "sea-grasses" (1906, pp. 401, 402) suggests that the Florida plant was probably some other species of this group. Temperature conditions favor West Florida as a possible locality for its growth. In his Flora of Bermuda, Britton (1918, p. 6) designates *Zostera marina* as a "native" plant, but the only specimen preserved in the herbarium of the New York Botanical Garden and labelled as from Bermuda consists of entangled leaves evidently cast ashore, but is supposed to have come from nearby shoals. It is to be noted that this specimen is plainly of the broad-leaved typical form of the species. It does not seem to occur in the Bahama Islands.

In attempting to deduce from the data of distribution as I have outlined them, the true conditions and laws of distribution of *Zostera marina*, there are certain considerations which stand out as of importance. I shall divide them under six heads, as follows:

(1) *Zostera marina*, as estimated taxonomically, probably consists of two or more genetic entities which seem to have

slightly different temperature relations, the narrow-leaved forms extending farther north than the broader-leaved forms;

(2) all forms of *Zostera marina* occupy shallow water in protected bays or inlets and, consequently inhabit the warmer waters of the zone or province they inhabit;

(3) it seems most probable to assume that the North Temperate Zone is the normal zone for *Zostera marina*, since a comparison of the distribution on all coasts indicates this zone rather than the North Subtropical or the Lower Boreal, the other two zones in which it is widespread;

(4) the southward invasion from the North Temperate Zone into the North Subtropical is not extensive on either the west coast of Europe or on the west coast of North America, but is extensive on the east coast of North America and on the east coast of Asia. The suggestion naturally is that these latter extensions are due to the greater deflections of the colder waters, as indicated by the lines of mean minima, on these coasts, *i.e.*, are seasonal invasions, e.g., chart 266 of B. M. Davis (1913, p. 536) indicates that *Z. marina* is an invader from colder waters at Woods Hole, Massachusetts;

(5) the invasions northward from the North Temperate Zone into the Boreal Zones are probably due to the localities, seemingly always situated at the innermost portions of long fiords, being raised in temperature (cf. Kjellman, 1883, p. 31) by the air temperature and by insolation;

(6) it may also be urged that the capacity of *Zostera marina* to continue its occupation of a particular locality and to spread to other even far distant localities, through its adaptions for floating and vegetative multiplication, may have some bearing on the extensive distribution of this species (cf. Ascherson, 1906, p. 402).

In conclusion, it may be well to summarize the principal points of general interest brought out or suggested, in the consideration of the marine spermatophytes.

1. The marine spermatophytes are largely made up of plants surrounded by a medium whose temperature at any given time is the same for all parts of the plant. The species of *Phyllospadix* alone present to a certain extent, at least, the temperature con-

ditions of terrestrial spermatophytes in that, at periods of low water, they have their roots in soil (or sand) of one temperature and their leaves in air of another. The majority of the marine spermatophytes live under a greater uniformity of temperature conditions than do the terrestrial spermatophytes.

2. The marine spermatophytes live under conditions very similar to those experienced by the marine algae and show the same temperature-zone relations as the marine algae.

3. The great majority of the species of the marine spermatophytes are confined strictly to one temperature zone of 5° C. amplitude of the monthly mean maximum of the surface waters. Such species are strictly stenothermal from every point of view and may be supposed to represent the normal type in distribution.

4. There are certain species which extend over two zones of temperature. It seems possible in these cases, as it has also seemed possible in the cases of certain marine algae, to regard these marine spermatophytes as normal to one zone whence they invade the other because they find in certain localities of the invaded zone their proper temperature, both as to intensity and duration. The invasions of the marine spermatophytes, like those of the marine algae, proceed in two directions in the cases of the two-zoned species, viz., from a warmer into a colder zone because of the existence of warmer spots among the colder areas normal to the zone, or from a colder into a warmer zone because of a seasonal lowering of the temperature of the warmer zone or portions of it.

5. There are a few species which are credited to more than two temperature zones and such are also found among the marine algae. It may be that these species being normal to one temperature zone, may invade not only one zone, but two or more additional zones because of the existence of localities or seasons of suitable temperature. This movement may be in only one direction from the normal zone, as in the case of *Halophila ovalis*, or it may be in two directions from the normal zone, as seems to be the case with *Zostera marina*.

6. Finally attention may be called to the difficulties attending the study of the distribution of a species caused by the incompleteness of our knowledge of its homogeneity or the lack of it,

its persistence through one or more seasons, its dependence upon spore reproduction or its ability to persist through vegetative multiplication, its seasons of flowering, fruiting, etc., in different portions of its range, any difference in habitat in different portions of its range, and any other matters which may be characteristic of the behavior of the species and which may possibly vary according to locality. The case of *Zostera marina* certainly indicates how much it is desirable to increase our knowledge of such species before we may feel certain that we are in any advantageous position to discuss the factors concerned in their very extensive distribution.

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